Territorial exclusion and reproductive isolation*

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Three experiments demonstrate that Mongolian gerbils exclude intruders from home territories and force them to migrate across a water barrier. Of those animals that did migrate in the third experiment, the majority avoided olfactory cues from the territory from which they were excluded.

The evolution of genetically distinct populations is commonly thought to require reproductive isolation of sufficient duration for the accumulation of genetic differences. The antecedents of the concept of reproductive isolation extends back to Aristotle. Isolation became a primary concept in Charles Darwin's demonstrations of natural selection and was elaborated on by Dobzhansky (1937) and Mayr (1970). The topic is still of great interest, as the exact mechanisms leading to reproductive isolation are not clear.

Recent evidence suggests that social behavior can be important in initiating isolation between gene pools. John J. Christian (1970), for example, has suggested that as population density increases, some animals are forced to migrate from the preferred habitat into unoccupied areas. This could lead to isolation from the core group and genetic differentiation. Miklos Udvardy (1970) contends, however, that migratory animals must become geographically isolated from the main group in order to prevent reciprocal gene flow. In other words, Christian's model could account for reproductive isolation only if it could be demonstrated that socially induced migration is across a geographical barrier.

ANIMALS AND APPARATUS

We have devised a laboratory model of social behavior and migration as a preliminary test of Christian's notions that will satisfy Udvardy's criterion of geographical isolation. The Mongolian gerbil (*Meriones unguiculatus*) is the species under study. The apparatus we use takes advantage of the tendency of gerbils to exclude intruders from their territory and sets up a natural water barrier between living areas. Basically, the living areas consist of two large boxes, 61 x 61 cm in area, one of which is divided by an opaque Lucite partition so that there are two compartments in one box and one compartment in the other. Both smaller living areas have doors opening onto an aquarium that is approximately 46 cm in length, beyond which is the larger living area.

Ordinarily, gerbils will not swim when given a reasonable choice. The question is, then, will animals choose to migrate across a geographical barrier when faced with animals holding and defending a territory? If they do, there is reason to conclude that territorial defense may be one form of social behavior that can stimulate migration of subordinate animals and establish reproductive isolation across an ecological barrier.

PROCEDURE AND RESULTS

We established a resident pair of adult gerbils (approximately 160 days of age) in one smaller living compartment and allowed it 2 weeks to establish its territory. Following this, 14 males and 14 females were individually introduced into the established territory over a period of 63 days. In order to verify that the intruders would not ordinarily swim, they were introduced into an empty living compartment 24 h before they were introduced to the resident pair. Each animal was then placed in the residents' territory for a maximum period of 24 h. During pretests, the animals were never observed to migrate.[1]

In all cases, fighting occurred when the intruders were introduced. Of the 28 animals introduced, 15 migrated across the aquarium to an empty compartment, 5 drowned in their attempts, 6 were killed in the residents' territory, and only 2 remained. Usually the battle was settled within an hour. There were no sex differences in the various categories, which was also the case in subsequent experiments.

In a replication of this same experiment, a new resident pair was tested against an equal number of males and females. The results were nearly identical, with 12 animals migrating, 3 drowning, 3 being killed, and 2 remaining in the territory. The comparability of the two experiments is seen in Fig. 1.

It appeared to us that both the male and female resident animals actively defended their territory, and that no intruder could have mated with any of the residents. Even those few individuals remaining in the territory were still under attack after 24 h. It seems reasonable to suppose, therefore, that territorial behavior leads to repulsion and dispersal severe enough to force territorial subordinates across a geographical barrier. In this situation, at least, the consequence is absolute reproductive isolation. The effect is not entirely laboratory-dependent, as we have seen comparable territorial defense and

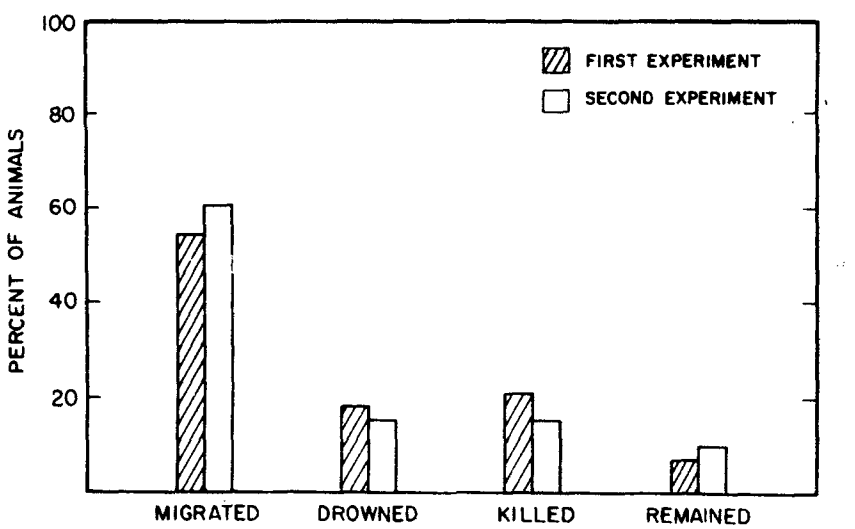

Fig. 1. Percent of intruders migrating, drowned, killed, and remaining in an occupied territory.

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active dispersal in an outdoor field situation.

We are now extending our investigations in an attempt to demonstrate that cues from territorial defenders are sufficient to reinforce isolation. Olfactory cues may be effective chemobarriers in gerbils, as they scent mark their territories and seem especially sensitive to this mode of communication (Nyby, Thiessen, & Wallace, 1970). Our initial attempt gives some support for this notion.

We first replicated the initial findings that territorial defense leads to migration and then tested the migrants in an olfactory choice situation during the next 24 h. The initial results were much the same as before. Of 10 males and 10 females introduced as intruders, 14 migrated, 1 drowned, and 5 remained in the residents' territory. The individual migrants were then given 24 h to choose between a cage with clean sawdust and one with excretions from the residents' living area. The two cages, each 34 x 29 x 15 cm in size, were connected with a short tunnel. Sawdust and contaminants from the residents' territory were placed daily under a wire mesh screen at the bottom of one cage, and clean sawdust was similarly placed in the other cage. Paper towels were provided in each cage as nesting material. Left-right positioning of the two types of sawdust was randomly alternated, as was the cage into which the intruder was placed. Fifteen animals that had never experienced encounters with the territorial pair received comparable 24-h tests.

At the end of 24 h, it was apparent that of those 11 Ss that showed a definite choice, 9 preferred to nest over the clean shavings rather than over shavings from the residents' territory ($\chi^2 = 4.46$, $df = 1$, $p < .05$). Two animals nested over the shavings from the territory. Three animals showed no obvious choice and were excluded from the analysis. Fifteen control animals showed random preference. It is tempting to suggest, therefore, that olfactory signals from territory-dominant animals can reinforce avoidance behavior and, hence, stabilize isolation of subordinate animals.

We are continuing our work on isolating mechanisms to demonstrate conclusively that territorial isolation is equivalent to reproductive isolation. Isoenzyme variations in plasma and tissue may offer us markers by which we can identify parents and populations. Using electrophoresis, we have identified an allelic variant, alpha-glycerophosphate-dehydrogenase, which may serve our purposes. Once the mode of inheritance is worked out for this enzyme, it should be possible to follow gene flow and differentiation between populations using this marker.

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NOTE

1. Longer periods have been tried at various times; we have never observed swimming when the animals were not under attack.